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Collembola in Norwegian coniferous forest soils
II. Vertical distribution

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With 7 figures

Contents

1. Introduction

This paper is the second contribution in a study of the Collembola fauna in Norwegian coniferous forest soils. The first dealt with the relations of Collembola with plant communities and soil fertility (Hågvar 1982), and a third will concern relations with soil chemistry.

In poor coniferous forest soils, the profile consists of very distinct layers. Because the needles decompose slowly, a thick raw humus layer is often formed. Below, a sharply defined bleached mineral layer may occur. However, in richer sites, brown earth profiles with mull humus can develop.

Information on the vertical distribution of Collembola in different soil profiles is desired for a better understanding of the function of these animals. Especially in podzol soils, needles and other above-ground litter slowly move down the profile as decomposition proceeds. In such a situation, the vertical position of a species may directly indicate the phase of decomposition in which it takes part.

In this investigation, the vertical distribution of single species as well as total Collembola and numbers of species have been described in seven different plant communities. The soils range from very poor iron podzols to a fertile brown earth (from Typic Udipsamment to Aquic Haploboroll, USDA classification).

Only a few studies from Scandinavia exist on the vertical distribution of Collembola in coniferous forest soils. Forsslund (1944) and Bödvarsson (1973) have presented some data from the organic layers in certain sites, but their extraction technique (Berlese funnel) is not strictly quantitative. The only quantitative (high-gradient) extractions of Collembola from different vertical layers in Scandinavian coniferous forest soils are those of Persson (1975); Leinaas (1976); Bengtsson & Rundgren (1980) and Persson et al. (1980). Howe-

ver, each of these treats only one forest type, and only the second and third paper consider vertical distribution at the species level. Furthermore, the present study includes deeper soil layers than those in the cited papers.

2. Description of habitats

The habitats were described by HÅGVAR (1982), and only the main points will be reviewed here. The sample plots were placed in corresponding vegetation types in two different study areas. Area A is situated near Ås, 30 km south of Oslo. Area B is located in Skrukkelia, 60 km north of Oslo. In area A, mean annual air temperature is 5.5 °C, and mean annual precipitation is 866 mm. Corresponding data for area B is 2.8 °C and 990 mm.

Detailed information on the vegetation was given by HÅGVAR (1982). Below, the vegetation types with abbreviations are listed according to increasing soil fertility: **(1)** Cladonio-Pinetum **(Cl-Pn)**; **(2)** Barbilophozio-Pinetum **(Ba-Pn)**; **(3)** Vaccinio-Pinetum **(Va-Pn)**; **(4)** Eu-Piceetum Myrtilletosum **(Eu-Pc My)**; **(5)** Eu-Piceetum Dryopteris **(Eu-Pc Dr)**; **(6)** Melico-Piceetum typical **(Me-Pc ty)**; **(7)** Melico-Piceetum Athyrium **(Me-Pc At)**.

In area A, two habitats with Me-Pc At vegetation were investigated. These were named A_1 and A_2. The soil in A_2 was unusually fertile and had a pH around 6.0, which is very high for a Norwegian coniferous forest.

Some of the main properties of the soils are presented in Table 1. A more detailed chemical description of all vertical layers will be given in a later paper where relations between Collembola and soil chemistry will be discussed. Soil profiles for each study plot are depicted in Fig. 1.

The soils in each area range from poor and very acid iron podzols with raw humus to fertile brown earths with mull humus and a comparatively high pH. Average sample depth is shown in Fig. 1. In area B, the podzol profiles were especially well developed, and both the raw humus layer (O_f/O_h) and the bleached layer (E) were thick. In the Ba-Pn site in area A, the soil had the character of peat.

A thin layer of ash was observed above the E layer in Eu-Pc My, area B, indicating a previous orest fire (see Fig. 1).

3. Material and methods

Each of the fifteen habitats was sampled in spring and autumn. The spring samples were taken just after snow melt in May/June and the autumn samples in August/September. Sampling dates have been given by HÅGVAR (1982).

At both sampling times at a given site, twenty soil cores were taken, each covering 10 cm². If possible, samples were taken down to 12 cm depth. The spring sample from Me-Pc ty in area A deviated by consisting of 11 samples of 33 cm². The depth on this occasion was limited to 9 cm although deeper samples would have been possible. All cores were divided into 3 cm thick sections, and extraction was performed according to MACFADYEN (1961).

The small Tullberginae were very numerous in all samples. Identification of these animals requires good slides and high magnification, and is very time-consuming. Therefore, the abundance data for species in the genera *Mesaphorura* (earlier named "*Tullbergia krausbaueri*"), *Wankeliella* and *Karlstejnia* had to be estimated from sub-samples. From each vertical layer at each sampling in a given site, about 60 random animals were identified (or all specimens if the total number was lower than 60).

For a more detailed description of material and methods, as well as some taxonomical remarks, see HÅGVAR (1982).

4. Results

4.1. Depth distribution of the most common species

In many species, large variations in depth distribution were observed between autumn and spring, and also between the different soils. However, these variations did not seem to form general patterns which could be related to season or soil type. In Fig. 2, therefore, only the mean vertical distribution of the most common species has been drawn. The presentation is based on all samples where the given species had a density of at least 1000 m⁻². For certain species occurring normally down to 9 or 12 cm, samples shallower than 12 cm were omitted from the calculations. More than half of the species usually had their maximum abundance in the upper 3 cm, and only four species occurred most numerously below the 6 cm depth.

Fig. 3 illustrates variations in vertical distribution between soils and seasons for three common species. Also the dominance values at each depth level have been indicated (black bars).

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Table 1. Some of the soil characteristics of the sampling plots. The dominant tree species is also indicated

Plant community		Cl-Pn		Ba-Pn		Va-Pn		Eu-Pc My		Eu-Pc Dr		Me-Pc ty		Me-Pc At		
Study area		A	B	A	B	A	B	A	B	A	B	A	B	A₁	B	A₂
Soil profile		Weakly developed iron podzol		Shallow peat		↑ (Weakly developed)		↑ (Weakly developed)		Brown earth	Iron podzol			↑ (Weakly developed)		
		←——————→				Iron podzol ←——————————————————————→						Brown earth ←·················→				
Humus type		Raw humus (crust)		Peat	Raw humus (felty)							Mull	Raw humus (granular)	Mull		
		←——————→			←——→									←··················→		
Soil pH	0—3 cm	3.74	3.70	3.65	3.79	3.85	3.98	3.65	3.79	4.18	4.20	4.35	5.22	4.16	5.58	5.88
	3—6 cm	3.76	3.83	3.42	3.55	3.62	3.59	3.32	3.44	3.90	3.73	3.89	5.21	4.10	5.54	6.09
	6—9 cm	—	3.90	3.50	3.59	3.63	3.77	3.45	3.54	3.91	3.73	3.92	5.24	4.16	5.44	6.05
	9—12 cm	—	—	3.56	3.97	3.91	3.88	3.69	3.67	4.03	4.16	3.94	5.31	4.17	5.48	5.99
Loss on ignation (%)	0—3 cm	71.8	51.3	95.3	92.5	78.9	72.7	79.7	91.1	49.6	80.0	77.0	67.4	19.3	79.7	11.2
	3—6 cm	27.6	14.4	79.1	50.0	36.3	16.9	25.0	45.1	23.7	25.5	29.0	58.6	12.6	56.9	9.4
	6—9 cm	—	3.2	51.2	21.5	13.9	4.7	7.4	9.0	14.2	8.6	15.6	52.9	9.0	39.9	9.9
	9—12 cm	—	—	48.3	9.1	7.8	3.6	5.4	6.0	10.0	9.5	10.7	46.2	6.4	30.2	9.1
Dominant tree species		*Pinus syl- vestris*	(Open area)	*Pinus syl- vestris*	*Picea abies* (scarce)	*Pinus syl- vestris*	*Betula pubes- cens*	*Picea abies* ←···→								*Fraxi- nus excel- sior*

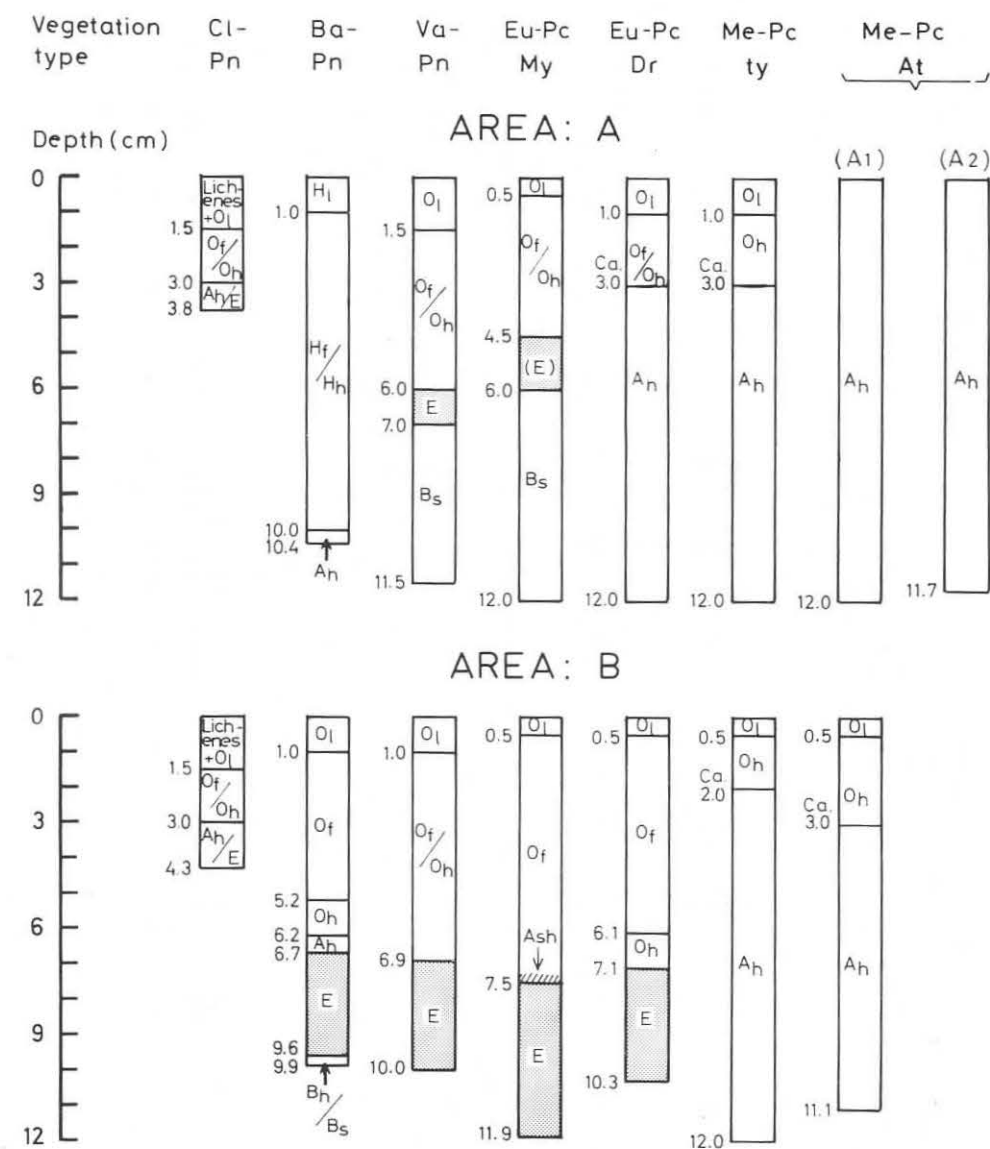Note: Raw humus types are according to DUMANSKI (1978).

Fig. 1. Soil profiles in the various habitats. Mean sampling depth is indicated (bottom figure in each profile). The bleached layers (E) in the podzol soils have been shaded. [O] organic horizon, [H] organic horizon rich in fine humus (here: peat-character), [A_n] mineral horizon with accumulation of organic matter (formed at or adjacent to the surface), [B_s] mineral layer below E, with sesquioxides, [B_h] corresponding layer with accumulation of organic matter. The suffix letters l, f and h in connection with O or H indicate litter, fermentation and humification, respectively. For further explanation of soil horizon terms, see DUMANSKI (1978) and Anonymous (1974).

Fig. 3. Variations in the vertical distribution of abundance (shaded columns) for three common species and total Collembola. Total abundance for all four depth levels is 100%. For total Collembola the black bars indicate the number of species, while for each species the black bars show the dominance at each depth level separately and [n] number of specimens. Abundance in thousands per m² "stone-free" soil is also indicated. Arrows show the deepest sampling level when 12 cm was not reached. On most sampling occasions, the number of cores from the deepest level was 15 or more. Stippled lines indicate uncertain data (only 6—8 samples, or less than 20 Collembola collected from a certain layer). Some habitats have been excluded due to insufficient data.

SPECIES	% in layers (20 40 60 80)	Depth cm	SPECIES	% in layers (20 40 60 80)
XENYLLA BOERNERI AXELSON — A = 1, B = 1, n = 430		3 6 9 12	WILLEMIA ANOPHTHALMA BÖRNER — A = 3, B = 7, n = 670	
LEPIDOCYRTUS LIGNORUM (FABRICIUS) — A = 7, B = 14, n = 958		3 6 9 12	ONYCHIURUS ARMATUS s.l. (TULLBERG) — A = 6, B = 25, n = 4005	
ISOTOMA HIEMALIS SCHÖTT — A = 2, B = 3, n = 235		3 6 9 12	ANURIDA FORSSLUNDI (GISIN) — A = 4, B = 7, n = 346	
ISOTOMA VIRIDIS BOURLET — A = 1, B = 2, n = 265		3 6 9 12	ISOTOMIELLA MINOR (SCHÄFFER) — A = 6, B = 23, n = 8018	
FOLSOMIA QUADRIOCULATA s.l. (TULLBERG) — A = 7, B = 22, n = 3826		3 6 9 12	MESAPHORURA SYLVATICA RUSEK — A = 4, B = 10, n = 568	
LEPIDOCYRTUS CYANEUS TULLBERG — A = 2, B = 3, n = 353		3 6 9 12	MESAPHORURA TENUISENSILLATA RUSEK — A = 6, B = 22, n = 1512	
ISOTOMA OLIVACEA TULLBERG — A = 4, B = 6, n = 730		3 6 9 12	NEELUS MINIMUS WILLEM — A = 3, B = 7, n = 297	
ONYCHIURUS ABSOLONI (BÖRNER) — A = 4, B = 6, n = 474		3 6 9 12	MESAPHORURA YOSII RUSEK — A = 4, B = 14, n = 1028	
ISOTOMA NOTABILIS SCHÄFFER — A = 5, B = 20, n = 4819		3 6 9 12	MESAPHORURA MACROCHAETA RUSEK — A = 2, B = 5, n = 306	
ANUROPHORUS SEPTENTRIONALIS PALISSA — A = 2, B = 3, n = 443		3 6 9 12	FOLSOMIA SENSIBILIS KSENEMAN — A = 4, B = 9, n = 1025	
ANUROPHORUS BINOCULATUS (KSENEMAN) — A = 6, B = 10, n = 1060		3 6 9 12	ANURIDA PYGMAEA (BÖRNER) — A = 4, B = 13, n = 1019	
HYPOGASTRURA INERMIS (TULLBERG) — A = 2, B = 3, n = 77		3 6 9 12	TULLBERGIA CALLIPYGOS BÖRNER — A = 1, B = 2, n = 87	
MESAPHORURA ITALICA RUSEK — A = 1, B = 2, n = 130		3 6 9 12	WANKELIELLA MEDIOCHAETA RUSEK — A = 1, B = 1, n = 27	
FRIESEA MIRABILIS (TULLBERG) — A = 7, B = 27, n = 2769		3 6 9 12	KARLSTEJNIA NORVEGICA FJELLBERG — A = 2, B = 3, n = 94	
WILLEMIA ASPINATA STACH — A = 3, B = 3, n = 108		3 6 9 12	TULLBERGIA QUADRISPINA (BÖRNER) — A = 1, B = 1, n = 23	
ISOTOMA SENSIBILIS (TULLBERG) — A = 1, B = 1, n = 64		3 6 9 12		

Fig. 2. Mean vertical distribution of the most common Collembola species. [A] number of plant communities from which data have been collected, [B] number of sampling occasions, and [n] number of animals.

FRIESEA MIRABILIS (TULLBERG) — **ISOTOMIELLA MINOR (SCHÄFFER)**

Below: Vegetation types	FRIESEA MIRABILIS (TULLBERG) Area A Spring	Area A Autumn	Area B Spring	Area B Autumn	DEPTH cm	ISOTOMIELLA MINOR (SCHÄFFER) Area A Spring	Area A Autumn	Area B Spring	Area B Autumn
Dom. in layers →	40 30 20 10	40 30 20 10	40 30 20 10	40 30 20 10		80 60 40 20	80 60 40 20	80 60 40 20	80 60 40 20
Relative abund. →	20 40 60 80	20 40 60 80	20 40 60 80	20 40 60 80		20 40 60 80	20 40 60 80	20 40 60 80	20 40 60 80
CI-Pn		14.8 n=128	6.8 n=130	4.2 n=79	3 6 9 12		2.2 n=16	3.0 n=47	1.9 n=24
Ba-Pn	5.9 n=114	6.5 n=120	6.3 n=124	6.8 n=135	3 6 9 12			4.0 n=75	7.8 n=153
Va-Pn	1.3 n=23	2.6 n=51	3.6 n=71	5.7 n=114	3 6 9 12	8.9 n=166	3.2 n=63	25.2 n=489	14.2 n=273
Eu-Pc My	3.0 n=59	3.6 n=70	11.2 n=223	12.9 n=244	3 6 9 12	9.6 n=184	13.5 n=270	18.6 n=370	20.5 n=389
Eu-Pc Dr	1.6 n=31	3.7 n=74	2.9 n=58	6.2 n=123	3 6 9 12	18.7 n=370	15.9 n=314	59.4 n=1158	14.3 n=277
Me-Pc ty	0.8 n=29	24.8 n=485	2.8 n=56	5.4 n=102	3 6 9 12	15.6 n=589	11.7 n=230	17.3 n=344	21.1 n=400
(A₁) Me-Pc At			1.4 n=26	2.1 n=39	3 6 9 12	45.7 n=913	26.0 n=517	24.8 n=488	16.3 n=312
(A₂)	1.5 n=28	1.7 n=33			3 6 9 12	10.0 n=195	3.5 n=68		

Below: Vegetation types	MESAPHORURA TENUISENSILLATA RUSEK				DEPTH cm	TOTAL COLLEMBOLA — Dark, thin columns: Number of species (upper scale)			
	Area A		Area B			Area A		Area B	
	Spring	Autumn	Spring	Autumn		Spring	Autumn	Spring	Autumn
Dom. in layers →	80 60 40 20	80 60 40 20	80 60 40 20	80 60 40 20		5 10 15 20	5 10 15 20	5 10 15 20	5 10 15 20
Relative abund. →	20 40 60 80	20 40 60 80	20 40 60 80	20 40 60 80		20 40 60 80	20 40 60 80	20 40 60 80	20 40 60 80

Cl-Pn: 17.2 n=69 ; 6.0 n=61 ; 12.4 n=68

Ba-Pn: 11.3 n=117 ; 7.0 n=52

Va-Pn: 11.6 n=89 ; 8.3 n=74 ; 4.7 n=44 ; 4.3 n=36

Eu-Pc My: 8.3 n=71 ; 7.6 n=76 ; 2.4 n=32 ; 4.5 n=31

Eu-Pc Dr: 3.9 n=70 ; 3.5 n=54 ; 11.5 n=87 ; 8.7 n=35

Me-Pc ty: 4.1 n=76 ; 9.9 n=84 ; 6.1 n=58 ; 13.9 n=100

(A₁) Me-Pc At: 8.1 n=128 ; 9.0 n=117 ; 5.9 n=100 ; 1.6 n=28
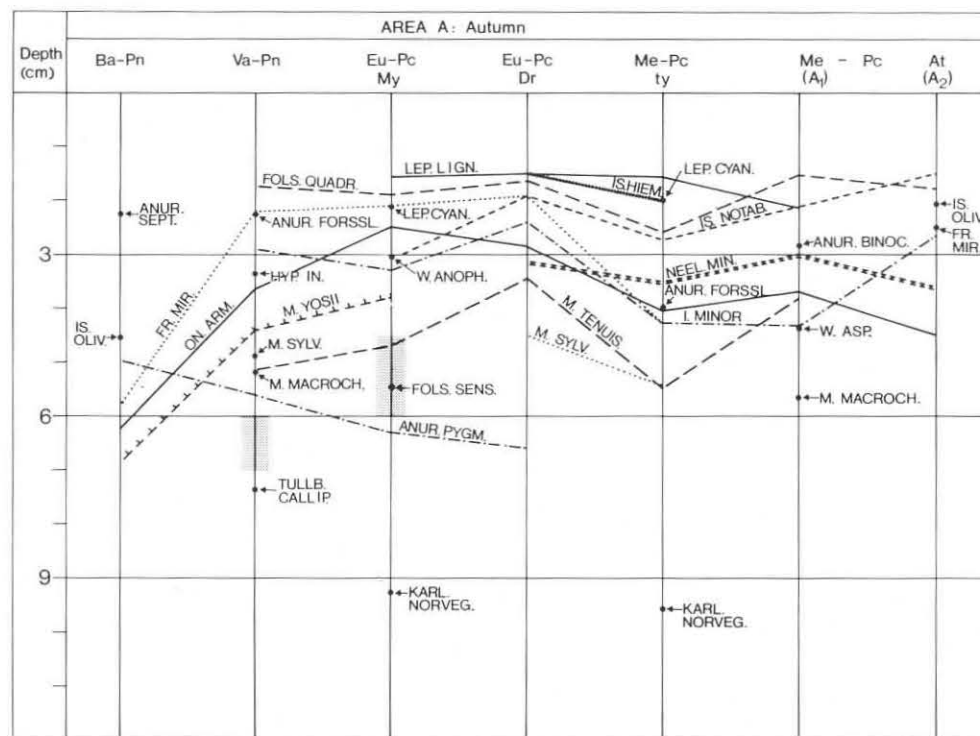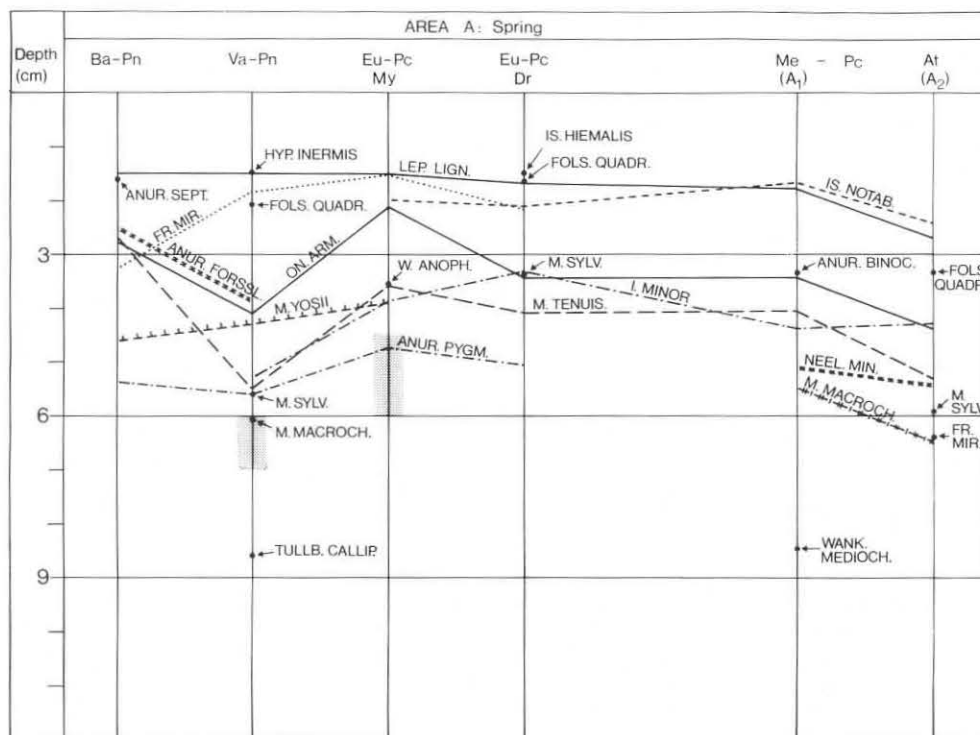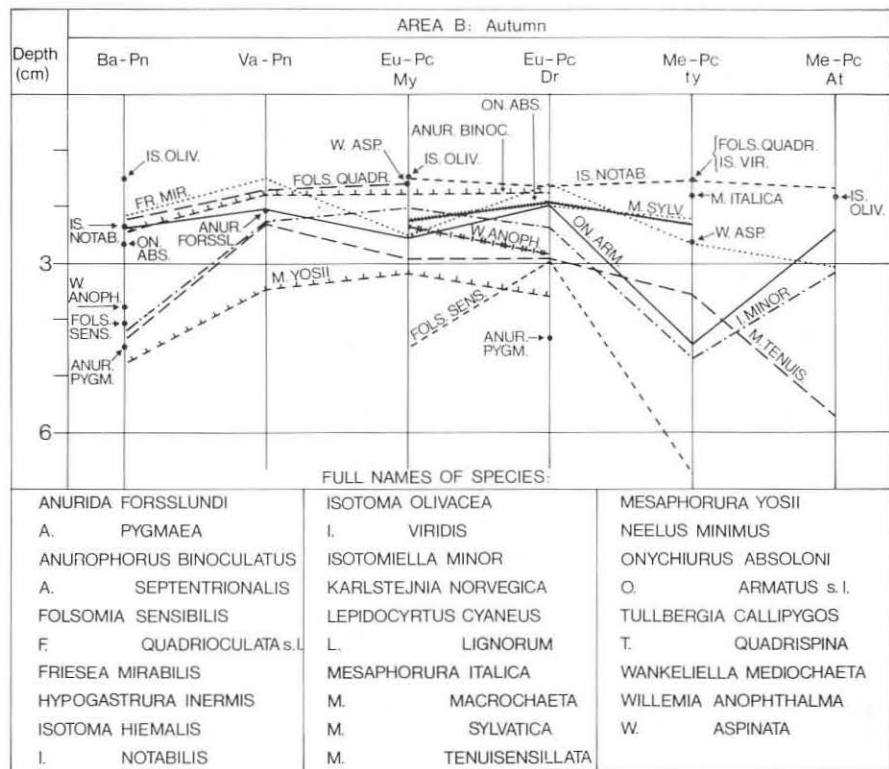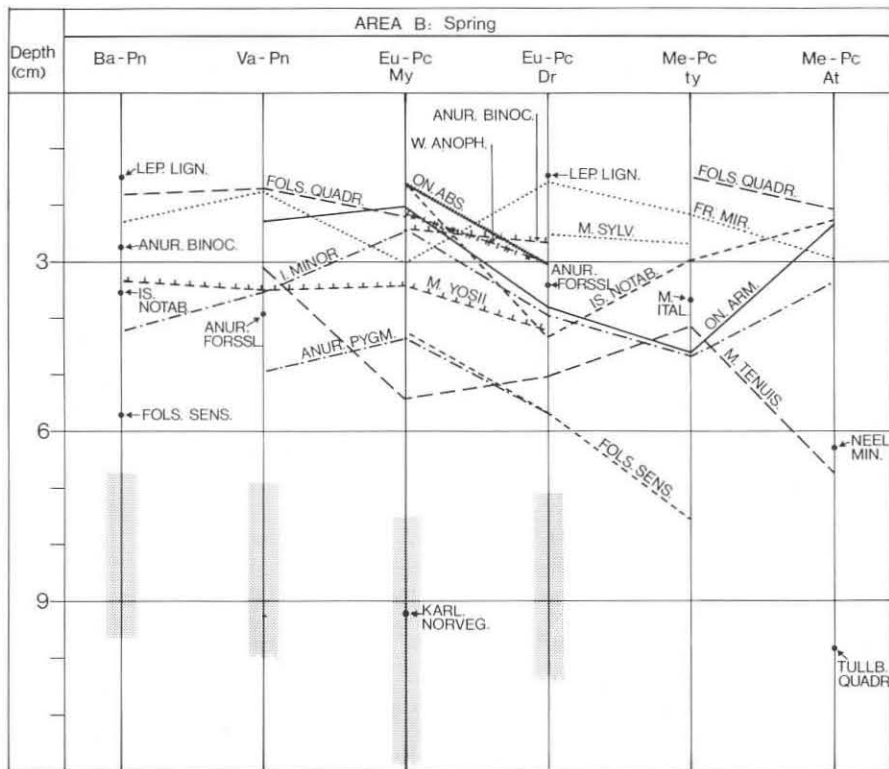
(A₂): 6.1 n=29

Fig. 3. (text p. 386)

Fig. 4 (two pages). Mean depth of the most common Collembola species in different habitats. Shaded areas indicate the extent of the bleached layer (E) in podzol soils. For further explanation see the text.

AREA B: Spring

AREA B: Autumn

FULL NAMES OF SPECIES:

ANURIDA FORSSLUNDI	ISOTOMA OLIVACEA	MESAPHORURA YOSII
A. PYGMAEA	I. VIRIDIS	NEELUS MINIMUS
ANUROPHORUS BINOCULATUS	ISOTOMIELLA MINOR	ONYCHIURUS ABSOLONI
A. SEPTENTRIONALIS	KARLSTEJNIA NORVEGICA	O. ARMATUS s. l.
FOLSOMIA SENSIBILIS	LEPIDOCYRTUS CYANEUS	TULLBERGIA CALLIPYGOS
F. QUADRIOCULATA s.l.	L. LIGNORUM	T. QUADRISPINA
FRIESEA MIRABILIS	MESAPHORURA ITALICA	WANKELIELLA MEDIOCHAETA
HYPOGASTRURA INERMIS	M. MACROCHAETA	WILLEMIA ANOPHTHALMA
ISOTOMA HIEMALIS	M. SYLVATICA	W. ASPINATA
I. NOTABILIS	M. TENUISENSILLATA	

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4.2. Depth distribution of total Collembola and number of species

At the bottom right in Fig. 3, the depth distributions of the total Collembola and number of species have been illustrated. Most samples revealed highest total abundance in the upper 3 cm. Between 3 and 12 cm depth, the total abundance always decreased for each successive depth level.

In most cases, the number of species also decreased gradually with increasing depth. However, the general picture is that the number of species was reduced more slowly than the abundance. In several cases, rather large numbers of species could be found in the 9—12 cm layer. Some of these values may also be underestimated, due to fewer samples from the deepest levels.

4.3. Mean depth in different soils

To facilitate comparisons between various species, soils and seasons, "mean depth" values have been calculated and drawn in Fig. 4. The mean depth is a theoretical figure and implies that the animals are considered to occur at the centre of each sample. In the present case, mean depth values can vary between 1.5 cm (all specimens in the upper section) and 10.5 cm (all specimens in the lowest section).

The concept is useful in several contexts and was also used by USHER (1970). If there are n_1 Collembola in the upper 3 cm, n_2 in the section below etc., the total number in a 12 cm deep core is $N = n_1 + n_2 + n_3 + n_4$. The "mean depth", M, is $M = \dfrac{1.5 \, n_1 + 4.5 \, n_2 + 7.5 \, n_3 + 10.5 \, n_4}{N}$.

Only samples including all four layers have been used, so the Cl-Pn habitats and the spring sampling in Me-Pc ty, area A, have been excluded from the analysis.

The main conclusions from Fig. 4 are:

(a) The average depth of practically all species is situated in the upper 6 cm in all soils. In podzol soils, only a few species had their mean depth in the mineral layers (E or below).

(b) Variation in mean depth between soils and seasons is generally least in species with the smallest mean depth (e.g. *Lepidocyrtus lignorum* and *Folsomia quadrioculata*).

(c) In some species, variation in mean depth may be considerable, between both soils and seasons.

(d) In most species, there is no consistent difference between mean depth in podzol soils and in brown earth soils.

(e) The vertical sequence of the species may show great variation, both between soils and seasons. Certain relative positions are, however, never broken. These cases will be discussed in section 4.5.

(f) Among the five closely-related *Mesaphorura* species, the relative vertical position varies greatly. However, *M. macrochaeta* always occur deepest (five observations, area A).

(g) On each sampling occasion, the average depth values for the different species are relatively evenly distributed in the range between 1.5 and 6 cm. Tendencies against compression of species, and also "empty" depth levels, can be observed, but on the whole a spacing of the mean levels is more typical than a clustering of them.

4.4. Life forms

Since there was no clear connection between soil type and the mean depth of each species, a generalized picture of the mean depth ranges for the various species has been drawn (Fig. 5). It should be pointed out that still larger ranges may exist for several of the relevant species, as the present picture refers to data from only two seasons.
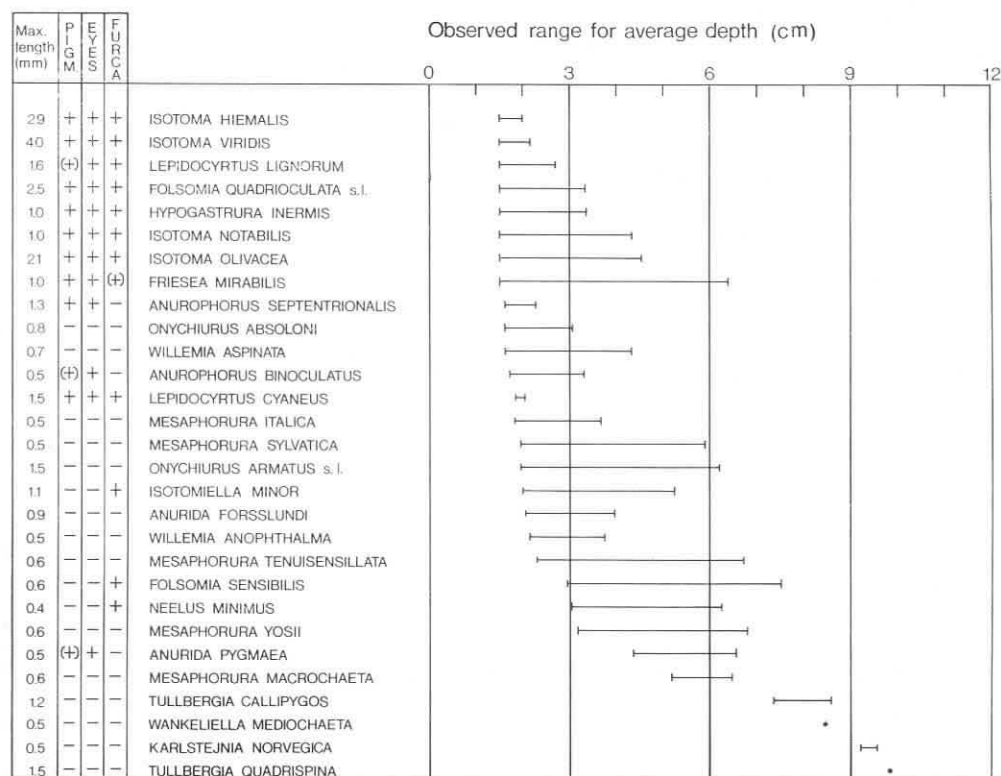
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Fig. 5. Observed range of average depth of the most common species, based on all sets of samples in different soils. Information on body length, pigmentation and the presence of eyes and furca are also given to illustrate the different "life forms".

It is evident from Fig. 5 that most species, at least periodically, may occur rather high up in the soil profile. Only eight species had their mean depth below 3 cm in all sets of samples, four had their range situated below 6 cm, and only two below 9 cm depth.

GISIN (1943) noted characteristic morphological changes in the Collembola species with increasing depth and defined different "life forms" on this basis. The present data confirm some of his main points. While surface-living species are large and have well-developed pigment, eyes and furca, deeper-living species tend to be small and colourless, without eyes or furca (Fig. 5).

4.5. A vertical hierarchy of species

In Fig. 5, many examples can be found of two species which have non-overlapping ranges for mean depth. The number of such species pairs is, however, greater than observed from this figure, since the relative position of two species in certain cases followed each other through the different soils (see especially the autumn samples in Fig. 4). By regarding the relative vertical position at each sampling occasion separately, relations were drawn between fourteen of the most common species (Fig. 6). Each pair of species connected by lines in the figure always had a constant relative position in terms of mean depth, whenever they occurred in the same soil. Because of a varying number of observations of the different species pairs, lines of different character have been used (see caption to Fig. 6). The connections drawn between species should be regarded as rigid bonds, keeping the relevant species separated with respect to mean depth.
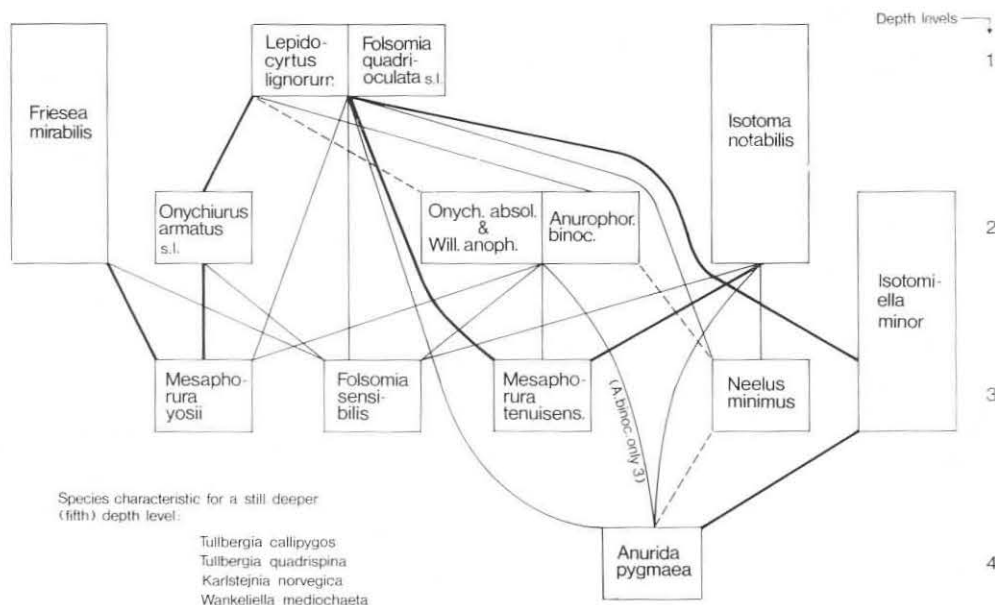
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Fig. 6. Vertical relationships between fourteen common species. Each pair of species connected by lines always had a constant relative position in terms of mean depths whenever they occurred in the same soil. Stippled lines: ≤ 3 observations; thin lines: 4—9 observations; thick lines: ≥ 10 observations. The species are naturally grouped into four "depth levels" ,whilst four less common species (not shown) would characterize a fifth depth level. Further explanation is given in the text.

A rather complex network of vertical relations appears in Fig. 6. However, the species naturally group themselves into four "depth levels". No consistent relations exist between species drawn at the same depth level. Three species, which showed great vertical plasticity, spanned two depth levels *(Friesea mirabilis, Isotoma notabilis* and *Isotomiella minor)*.

The two typical inhabitants of the upper level *(Lepidocyrtus lignorum* and *Folsomia quadrioculata)*, showed many consistent relationships with other species. Three species in the second depth level could also in several respects be considered as a unit *(Onychiurus absoloni, Willemia anophthalma* and *Anurophorus binoculatus)*. The fourth level is characterized by the small species *Anurida pygmaea*. To this should be added a fifth depth level, in which some typical deep-living, but less abundant, species occur: *Tullbergia callipygos, T. quadrispina, Karlstejnia norvegica* and *Wankeliella mediochaeta*.

4.6. The Collembola fauna of the bleached layer

In four vegetation types in area B, the bleached layer (E) was especially well developed (cf. Fig. 1). The species encountered in this layer in the spring samples are listed in Table 2. Evidently this minerall ayer is poor in species and contains mainly small Collembola which are able to inhabit narrow cavities.

Rather large numbers of species were often noted in deeper levels in podzol soils (Fig. 3) because the raw humus layer in certain cores penetrated down to 9 or 12 cm. At a certain depth level, the Collembola fauna depended on the proportion of raw humus present. This has been illustrated in Fig. 7. In four podzol soils, abundance and number of species in the 6—9 cm layer have been related to the volume percentage of raw humus in each core from this depth. In all sites, there was a trend towards increasing abundance and number of species with increasing raw humus content. Variation was large, and in some cases a pure bleached layer sample could contain more animals or species than a pure raw humus sample from the corresponding depth. However, in all cases, the regression analysis showed significant slope (see P-values in Fig. 7).
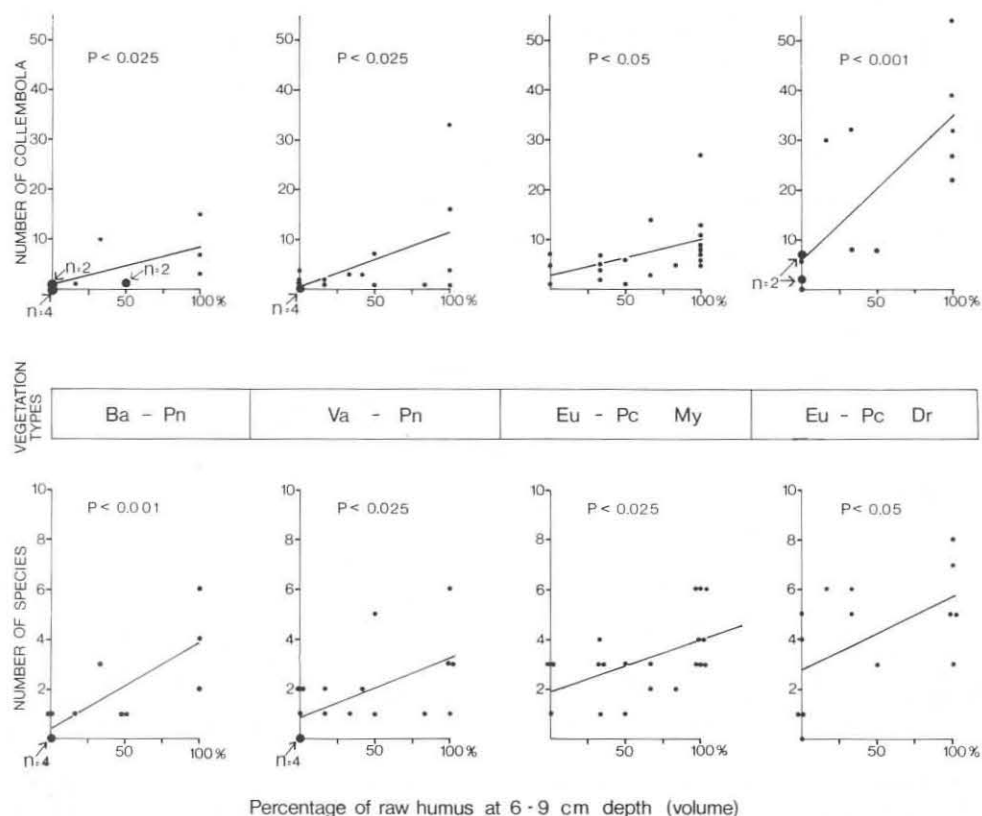
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Fig. 7. The number of individuals and species of Collembola, in the 6—9 cm layer of some podzol soils, related to the volume percentage of raw humus in the core (0% means a pure bleached-layer sample). The data are from the spring samples in area B. Regression lines have been drawn, and the significance of the slopes are given.

Table 2. Collembola species found in the bleached layer (E) in podzol soils (spring, area B)

Species	Vegetation type			
	Ba-Pn	Va-Pn	Eu-Pc My	Eu-Pc Dr
Anurida forsslundi	×	×		
Mesaphorura yosii	×		×	
Folsomia sensibilis	×		×	×
Mesaphorura tenuisensillata		×		
Anurida pygmaea		×	×	
Folsomia quadrioculata s. l.		×		
Mesaphorura sylvatica		×		
Isotomiella minor		×		×
Karlstejnia norvegica			×	
Friesea mirabilis			×	
Anurophorus binoculatus				×

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Table 3. The abundance of different Collembola species at various depth levels in an abnormal sample (10 cm²), compared with normal conditions (Me-Pc ty, autumn, area B)

Speceis	Numbers in the abnormal sample				Normal numbers per sample			
	Depth (cm)				Depth (cm)			
	0—3	3—6	6—9	9—12	0—3	3—6	6—9	9—12
Mesaphorura sylvatica	0	5	171	670	4	1	<1	0
M. tenuisensillata	32	48	86	37	8	3	2	1
M. cf. sylvatica	33	48	34	24	2	1	0	0
M. italica	7	2	0	0	9	1	0	<1
Willemia anophthalma	8	0	19	86	<1	0	<1	<1
Onychiurus armatus s. l.	16	15	14	5	3	1	1	1
Willemia aspinata	8	2	4	5	2	<1	<1	<1
Friesea mirabilis	2	2	0	0	4	1	<1	<1
Isotomiella minor	5	4	1	0	8	6	5	2
Isotoma notabilis	1	0	0	0	5	<1	0	0
Onychiurus absoloni	1	0	0	0	1	0	<1	0
Total Collembola	**113**	**126**	**329**	**827**	**54[1]**	**16[1]**	**11[1]**	**6[1]**

[1] Including some additional species.

4.7. An abnormal sample

A highly abnormal sample, which was collected in the autumn in Me-Pc ty, area B, deserves to be mentioned. Data from this single core have not been included in the previous analyses.

A full survey of species and numbers from all four depth levels in this core is shown in Table 3, together with normal values. While the species composition was as expected, some species attained extraordinarily high densities. Furthermore, the abundance of several species increased with depth. The most extreme was *"Tullbergia krausbaueri"*. According to recent systematics, this taxon should be divided into several *Mesaphorura*-species, of which *M. sylvatica* proved to be mainly responsible for the large numbers in the deeper layers. *M. tenuisensillata* and *M. cf. sylvatica* were numerous in all layers. However, a fourth species in this genus, *M. italica*, showed quite normal densities. *Willemia anophthalma* was another species with unusually large abundance at 9—12 cm, while *Onychiurus armatus* s. l. was unusually abundant in the upper 9 cm. Total Collembola abundance in all layers was about 1400 per 10 cm² compared with a normal density of 87 per 10 cm².

5. Discussion
5.1. General patterns of vertical distribution

Other "high gradient" extractions from Scandinavian coniferous forest soils confirm that the upper few centimeters of the profile (except for the superficial litter layer) support the highest concentrations of Collembola (PERSSON 1975; LEINAAS 1976; BENGTSSON & RUNDGREN 1980). Numerous investigations from a variety of soils (although using different extraction techniques) indicate that this is a general pattern for Collembola (e.g. VOLZ 1934; GLASGOW 1939; FORSSLUND 1944; WEIS-FOGH 1948; SCHALLER 1949; DRIFT 1951; HAARLØV 1955; SHEALS 1957; PALISSA 1959; HAARLØV 1960; HÜTHER 1961; POOLE 1961; DHILLON & GIBSON 1962; MILNE 1962; CHRISTIANSEN 1964; MADGE 1965; HALE 1966; WOOD 1967; MARSHALL 1974; PERSSON & LOHM 1977; TAMURA & CHIBA 1977; TAKEDA 1978). As pointed out by several of these authors, and also in the synthesis by WALLWORK (1970), the largest populations are usually located at the level where the most active decomposition of organic material is occurring. In podzol soils this level is termed the "fermentation" zone (O$_f$) and lies between the litter layer (O$_l$) and the humus layer (O$_h$) (cf. Fig. 1). HAARLØV (1955) pointed out that this layer is the optimal one for microarthropods for several reasons: food is abundant, the pore space system is suitable and allows the individuals to move rather freely, and the layer is rather resistant to desiccation.

The number of species, however, decreased more slowly than the abundance with increasing depth. This is confirmed by Swedish studies in several spruce forest sites, where samples were taken at 0—2, 2—4 and 4—10 cm depth (BENGTSSON & RUNDGREN 1980). Also PRAT & MASSOUD (1980) observed this relation in a mixed forest in France. Clearly, the deeper layers may be quite rich in niches. A combination of many species and low total abundance is often seen between 3 and 12 cm depth in the present data (Fig. 3).

The vertical distribution of typical hemiedaphic species (large, pigmented, with eyes and furca) and euedaphic species (small, unpigmented, without eyes and furca) overlapped considerably (Fig. 5). However, the characteristic hemiedaphic species occurred mainly in the upper 3 cm of the soil. The four deepest-living species were typical euedaphic forms, except that two of them can grow to a length above 1 mm (Fig. 5). As shown by HAARLØV (1955, 1960) and later confirmed by others (e.g. DHILLON & GIBSON 1962; TAKEDA 1978), the soil porosity decreases with depth. HAARLØV (1955) showed that only microarthropods of small diameter inhabited the soil below certain depths. In the present material, all eight species with mean depth levels consistently below 3 cm have small body diameters, and all but *Neelus minimus* and *Anurida pygmaea* have the slender, elongated body shape characteristic for Tullberginae. Probably body diameter rather than body length should be used in the characterization of "life forms".

Several small and morphologically euedaphic species, for example *Onychiurus absoloni* and *Willemia aspinata*, often occur high up in the profile (Fig. 5). This feature has been observed by several authors (e.g. HAARLØV 1955 and 1960; LEINAAS 1976; TAKEDA 1978).

Fig. 6 indicates that the relative vertical position of several common species (defined from mean depth) seems to be stable, at least during the two seasons sampled. It is interesting that the species arrange themselves into as many as five "depth levels". Pore volume and drought resistance certainly contribute to this system. Among several other factors, competition may promote vertical segregation. It is noteworthy that closely-related and morphologically similar genera may inhabit quite different depth levels (*Mesaphorura* in the third depth level and *Tullbergia*, *Karlstejnia* and *Wankeliella* in the fifth depth level).

5.2. Flexibility in vertical distribution

The variation in vertical distribution between seasons and soils is probably regulated by a large number of factors. Investigators as early as VOLZ (1934); GLASGOW (1939); AGRELL (1941); SCHALLER (1949) and STRENZKE (1949) assumed that Collembola actively migrated to deeper levels during drought and low temperatures. Several recent high-gradient extractions have confirmed seasonal variations in the vertical distribution of total Collembola and single species (e.g. HALE 1966; USHER 1970; MARSHALL 1974; LEINAAS 1976; PERSSON & LOHM 1977). In Norwegian spruce forest, LEINAAS (1976) demonstrated that many species actively migrate to deeper levels in winter. It has also been shown that juvenile specimens often live deeper than adults of the same species (AGRELL 1934 and 1941; WEIS-FOGH 1948; MILNE 1962; WALLWORK 1970; FJELLBERG 1974; PERSSON & LOHM 1977; PETERSEN 1980). This induces variation in depth distribution according to the life cycle of each species.

Many authors have observed that Collembola species can adjust their depth distribution according to local soil conditions (e.g. BELLINGER 1954; BOCKEMÜHL 1956; PALISSA 1959; HÜTHER 1961; LEUTHOLD 1961; CHRISTIANSEN 1964; WOOD 1967; BÖDVARSSON 1973). In the present investigation, the loss on ignition data (Table 1), combined with a visual evaluation of soil profiles, strongly indicates that pore volume at 6—12 cm depth was greatest in the peat soil (Ba-Pn, area A) and in the two brown earths in area B (Me-Pc ty and Me-Pc At). It is seen from Fig. 4 that the few cases of especially high mean depth values were observed in these three soils (*Friesea mirabilis*, *Onychiurus armatus s.l.* and *Mesaphorura yosii* in the peat soil during autumn; and *Folsomia sensibilis* and *Mesaphorura tenuisensillata*, each in one of the relevant brown earth soils in both seasons).

The abnormal sample demonstrates that depth itself is no limiting factor for Collembola in the upper 12 cm. The relevant core had an unusually light colour below 6 cm depth.

Specimens of the very abundant species *Mesaphorura sylvatica* had their guts filled with fungal hyphae at 9—12 cm depth. A locally rich nutrient source may have induced the abnormally large populations. In general it may be postulated that food is the main limiting factor at greater depths.

We may conclude that depth is only one of many niche dimensions for soil Collembola. By vertical migration, each species probably tries continually to optimize its life and reproductive conditions. In this way, the realized niche may vary between seasons and soil types. This flexibility implies that a single set of samples from a certain habitat gives only a transient picture of the Collembola fauna at different depth levels.

5.3. The Collembola fauna of the mineral soil

Several investigations have shown that the mineral soil below the organic layers contains a rather specific Collembola fauna consisting mainly of small, white species. Species commonly mentioned are "*Tullbergia krausbaueri*" (including the *Mesaphorura* species and perhaps other genera of Tullberginae), *T. callipygos, Anurida pygmaea, Folsomia sensibilis, Isotomiella minor* and *Friesea mirabilis* (SCHALLER 1949; POOLE 1961; LEINAAS 1976; PRAT & MASSOUD 1980). In addition, some specimens of hemiedaphic species may occur, but probably often in juvenile stages due to the small pore spaces in the mineral soil. The species composition from the bleached layer in the present study (Table 2) has a character which conforms well with earlier investigations.

While the boundary between the organic layer and the bleached layer may be quite sharp in podzol soils, the change in the Collembola fauna is more gradual. Generally, lower abundance and numbers of species are found in the bleached layer, but certain bleached layer samples may contain a number of species and animals comparable to raw humus conditions (Fig. 6). Perhaps dead roots in this layer may represent locally rich food sources.

5.4. Depth distribution of single species

Due to the great ability of most species to change their depth distribution, a detailed comparison with earlier studies is not desirable. However, the overall results reported here are in accordance with the literature. It is interesting that two of the deepest-living species in the present study, *Tullbergia callipygos* and *T. quadrispina*, have been found also in several other investigations to belong to the most deep-living Collembola communities (FRENZEL 1936; GLASGOW 1939; SCHALLER 1949; BOCKEMÜHL 1956; HÜTHER 1961; LEUTHOLD 1961; POOLE 1961; USHER 1970; PERSSON & LOHM 1977; PETERSEN 1980; PRAT & MASSOUD 1980). Earlier studies in Norwegian coniferous forests confirm the deep-living character of two other species: *Folsomia sensibilis* (LEINAAS 1976) and *Karlstejnia norvegica* [HÅGVAR unpubl.].

Several of the *Mesaphorura* species (perhaps all) are parthenogenetic in forest soil (PETERSEN 1971 and 1978), and the species concept is not strictly valid. The validity of the splitting of *Tullbergia krausbaueri* s.l. can best be checked through the ecology of the various "species" or forms. HÅGVAR (1982) showed that the five *Mesaphorura* species in Fig. 5 were distributed differently in the various vegetation types of coniferous forest. Vertically, however, only *M. macrochaeta* showed a characteristic position by having the deepest mean value whenever it occurred together with other *Mesaphorura* species. In a Swedish study in spruce forest, where the corresponding species except *M. italica* were found together, all species occurred mainly in the 0—2 cm layer (BENGTSSON & RUNDGREN 1980).

The abnormal sample may, however, contribute to a clarification. Here, four *Mesaphorura* "species" showed different vertical distributions. The marked difference between *M. sylvatica* and *M. cf. sylvatica* indicate that even these very similar forms have different ecologies (see HÅGVAR 1982 for the distinction between these). *M. italica* was most common in the 0—3 cm layer, *M. cf. sylvatica* in the 3—6 cm layer, *M. tenuisensillata* in the 6—9 cm layer and *M. sylvatica* in the 9—12 cm layer (Table 3). Perhaps the species become more clearly separated vertically during times of maximum population density.

6. Résumé

[Les collemboles des forêts de conifères en Norvège
II. Distribution verticale]

La distribution verticale des Collemboles a été étudiée dans 7 types différents de végétation dans une forêt de conifères au SE de la Norvège. Des échantillons (si possible de 12 cm de profondeur) ont été collectés au printemps et en automne dans deux sites d'étude, chacun comprenant tous les types de végétation. Les sols variaient du podzol peu développé à humus brut au sol brun riche à mull.

La profondeur moyenne de pratiquement toutes les espèces était située dans les 6 cm supérieurs des sols; cette profondeur était inférieure à 6 cm pour seulement quatre espèces des podzols occupant la couche minérale *(Tullbergia callipygos, T. quadrispina, Karlstejnia norvegica* et *Wankeliella mediochaeta)*. Les espèces avaient des distributions verticales différentes en fonction des sols et des saisons à l'axception d'espèces de grande taille confinées à la surface. Une amplitude verticale caractéristique peut être indiquée pour beaucoup d'espèces. Les zones propres aux expèces hemiédaphiques et euédaphiques se recouvrent largement. Pour la plupart des espèces, il n'y a aucune différence notable en profondeur moyenne entre le podzol et le sol brun.

La position verticale relative des différentes espèces (fondée sur la profondeur moyenne) était plutôt flexible, tant entre sols qu'entre saisons. Certains positions relatives n'étaient néanmoins jamais tranchées. Un système de cinq ,,niveaux biologiques de profondeur", chacun avec des espèces caractéristiques, est proposé.

Un grand nombre de facteurs influencent probablement la position verticale d'une espèce. Ceci indique que chaque espèce adapte constamment sa distribution verticale afin d'optimiser sa reproduction et ses conditions vitales. Ceci implique que la structure d'une communauté subit constamment des changements verticaux. Un prélèvement d'échantillon unique d'un habitat particulier ne reflète que fugitivement les différents niveaux de profondeur de la faune de Collemboles.

Mots-clé: Collemboles, forêts conifères, distribution verticale, types de végétation, types de sol.

7. Acknowledgements

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The vertical distribution of Collembola was studied in seven different vegetation types in coniferous forest of SE Norway. Samples (down to 12 cm if possible) were taken in spring and autumn in two different study areas, each containing all the relevant vegetation types. The soils varied from poor and acid podzols with raw humus, to rich brown earths with mull humus.

The average depth of practically all species was situated in the upper 6 cm in all soils. In podzol soils, only four species *(Tullbergia callipygos, T. quadrispina, Karlstejnia norvegica* and *Wankeliella mediochaeta)* had their mean depth consistently below 6 cm, i.e. in the mineral layer. Except for the larger species restricted to the surface layers, many species showed considerable variation in depth distribution between both soils and seasons. Still, certain characteristic vertical distributions could be demonstrated for many species. A considerable overlap existed between hemiedaphic and euedaphic species. In most species, there was no consistent difference between mean depth in podzol and brown earth soils.

The relative vertical position of the different species (based on average depth) was rather flexible, between both soils and seasons. Certain relative positions were, however, never broken. A system of five depth levels, each with characteristic species, was recognized and described. A large number of factors probably influence the vertical position of a species. It is suggested that each species continually adjusts its vertical distribution in order to optimize its life and reproductive conditions.

This also implies that the community structure continually undergoes vertical changes. A single sample from a habitat gives only a transient picture of the Collembola fauna at different depth levels.

Key words: Collembola, coniferous forest, vertical distribution, vegetation types, soil types.